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Key Points:
- Marine N_2 fixers can successfully compete in N-rich environments
- Observed patterns of marine N_2 fixation in the North Atlantic can be explained
- Iron limitation enhances P* fluxes in oligotrophic regions

Supporting Information:
- Figures S1–S7 and Table S1

Correspondence to:
A. Landolfi,
alandolfi@geomar.de

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A new perspective on environmental controls of marine nitrogen fixation

A. Landolfi[1], W. Koeve[1], H. Dietze[1], P. Kähler[1], and A. Oschlies[1]

[1]GEOMAR Helmholtz-Zentrum für Ozeanforschung, Marine Biogeochemical Modelling, Kiel, Germany

Abstract Growing slowly, marine N_2 fixers are generally expected to be competitive only where nitrogen (N) supply is low relative to that of phosphorus (P) with respect to the cellular N:P ratio (*R*) of nonfixing phytoplankton. This is at odds with observed high N_2 fixation rates in the oligotrophic North Atlantic where the ratio of nutrients supplied to the surface is elevated in N relative to the average *R* (16:1). In this study, we investigate several mechanisms to solve this puzzle: iron limitation, phosphorus enhancement by preferential remineralization or stoichiometric diversity of phytoplankton, and dissolved organic phosphorus (DOP) utilization. Combining resource competition theory and a global coupled ecosystem-circulation model, we find that the additional N and energy investments required for exoenzymatic breakdown of DOP give N_2 fixers a competitive advantage in oligotrophic P-starved regions. Accounting for this mechanism expands the ecological niche of N_2 fixers also to regions where the nutrient supply is high in N relative to *R*, yielding, in our model, a pattern consistent with the observed high N_2 fixation rates in the oligotrophic North Atlantic.

1. Introduction

Nitrogen fixation is essential for maintaining the marine fixed nitrogen (N) inventory which regulates ocean productivity. In spite of its importance, environmental controls of marine N_2 fixation are not well understood. Nutrient requirements and the ability to compete for limiting nutrients strongly affect the regional distribution of different phytoplankton functional types in the ocean [*Tilman*, 1980; *Dutkiewicz et al.*, 2012; *Ward et al.*, 2013]. N_2 fixers are not limited by dissolved inorganic nitrogen such as nitrate and ammonium because they can utilize the abundant N_2, albeit at a high energetic cost. When considering competition for N and P, resource competition theory [*Tilman*, 1980; *Ward et al.*, 2013] predicts that in steady state systems, P-limited N_2 fixers may coexist with N-limited nonfixing phytoplankton only where the N supply is low relative to the supply of P with respect to the cellular N:P ratio of nonfixing phytoplankton (*R*) (Figure 1a, $N{:}P_{supply} < R$), i.e., where positive P*, defined as $P^* = PO_4^{3-} - NO_3^-/R$, is supplied. As N_2 fixers grow and add N to the system, they consume P* thus narrowing their own niche (Figure 1a, reduce α). Then, why do N_2 fixers successfully compete and exhibit high rates of N_2 fixation in the oligotrophic North Atlantic (Figure 2a) [*Capone et al.*, 2005; *Großkopf et al.*, 2012; *Luo et al.*, 2012], where the nutrient supply is high in N relative to *R*? Here the ratio of nutrients supplied to the euphtotic zone, from the thermocline [*Gruber and Sarmiento*, 1997] and from atmospheric deposition [*Krishnamurthy et al.*, 2009], is well above the average *R* (N:P = 16), and the estimated P* flux [*Palter et al.*, 2011] is not sufficient to fuel N_2 fixation observational estimates ($\geq$20 Tg N yr^{-1}, Table 1). N_2 fixers have a high iron requirement [*Kustka et al.*, 2003], and the high aeolian iron inputs into the North Atlantic [*Mahowald et al.*, 2005] are thought to favor N_2 fixation there [*Moore et al.*, 2009; *Schlosser et al.*, 2014]. Preferential remineralization of phosphorus [*Landolfi et al.*, 2008] and the utilization of dissolved organic phosphorus (DOP) by diazotrophs [*Dyhrman et al.*, 2006; *Sohm and Capone*, 2006] have also been suggested to support N_2 fixation in the North Atlantic [*Coles and Hood*, 2007]. The ability to competitively hydrolyze semilabile DOP [*Sohm et al.*, 2008; *Orchard et al.*, 2010; *Orcutt et al.*, 2013] and access the more refractory phosphonates [*Dyhrman et al.*, 2006] may be the key to diazotrophs's success in P-depleted environments. P depletion demands greater N investments into nutrient uptake machinery (e.g., enzymes that, being proteins, contain N and little P) at the expense of cell growth [*Klausmeier et al.*, 2004]. Diazotrophs' unlimited access to N_2 may hence explain their competitive ability to exploit the DOP reservoir better than nonfixing phytoplankton. Such a mechanism has been suggested to explain the occurrence of N_2 fixing plants in phosphorus-limited terrestrial ecosystems [*Houlton et al.*, 2008].

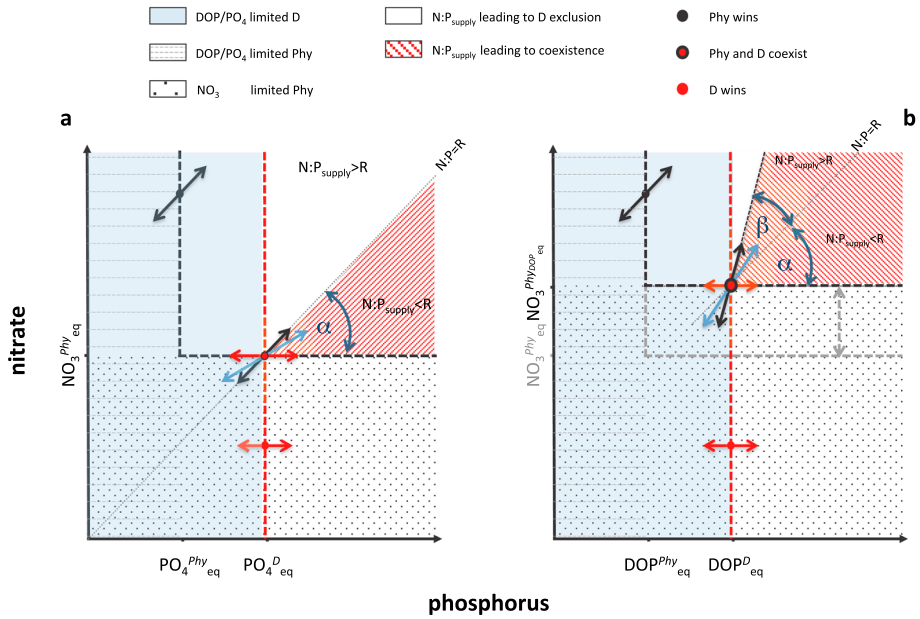

Figure 1. Illustration of the resource competition theory [*Tilman*, 1980]. Nonfixing phytoplankton (Phy, black) and diazotrophs (D, red) grow drawing down nutrient concentrations to their equilibrium nutrient requirements (NO_{3eq}, PO_{4eq}, and DOP_{eq}) reaching steady state (growth balanced by mortality) on the zero net growth isoclines (ZNGI, black and red dashed lines). If nutrient concentrations are drawn below the algae equilibrium requirement, their growth is limited by nutrient availability (shaded areas) and the algae will be competitively excluded (mortality > growth). Stable coexistence (red-and-black circle) of Phy and D occurs at the interception of the ZNGIs where the growth of Phy is limited by NO_3 and that of D is limited by PO_4. (a) Phy consume resources (black arrow) in their cellular (R) proportions (i.e., following the slope of the thin black dotted line N:P= R, where R can differ from 16:1). D consume only phosphate (red arrow). Blue arrows pointing toward the axis origin are the total nitrate and phosphate consumption vectors that, at steady state, are balanced by the nutrient supply vectors (pointing away from the axis origin). For $N:P_{supply} < R$, i.e., region α, nitrate concentrations will be drawn down to NO_{3eq}^{Phy} by Phy and phosphate to $PO_{4eq}{}^{D}$ by D leading to the stable coexistence (red-and-black circle). The larger the R, the larger is the coexistence region (larger α). For $N:P_{supply} > R$ both species are limited by PO_4, and Phy, with the lowest PO_{4eq}, reduce phosphate concentrations too low for the survival of D (black dot). D outcompete Phy where nitrate concentrations are too low to meet $NO_3^{Phy}{}_{eq}$ (red dot). (b) When accounting for the extra energetic and N costs for DOP uptake, Phy require higher nitrate at equilibrium ($NO_3^{Phy_{dop}}{}_{equ} > NO_3^{Phy}{}_{equ}$, grey arrow) increasing the nitrate-limited growth area (dotted area) and consume nitrate (black arrow) in proportions exceeding R. The region of coexistence becomes larger ($\alpha + \beta$), and D can survive also for $N:P_{supply} > R$ (β). Details are in the supporting information.

Using both resource competition theory and a three-dimensional global biogeochemical circulation model, we investigate how the above factors affect the distribution of modeled N_2fixation and assess mechanisms capable of expanding the ecological niche of N_2fixers in a way to allow N_2fixation in the P-starved oligotrophic North Atlantic.

2. Methods

The global ocean circulation model employed is based on MOM4, CM2.1 setup [*Gnanadesikan et al.*, 2006], configured on a 3°×2° grid, forced by monthly heat, freshwater fluxes, and wind fields taken from the climatological data set of the Coordinated Ocean Reference Experiments [*Large and Yeager*, 2004]. Initial annual mean temperature and salinity are from the World Ocean Atlas [*Conkright et al.*, 2002]. The circulation model is coupled online to a modified version of the ecosystem model of *Schmittner et al.* [2008] as described in *Landolfi et al.* [2013] initialized with observed nutrient and oxygen distributions [*Conkright et al.*, 2002]. Briefly, the ecosystem model (details are in the supporting information) has 10 prognostic variables: dissolved oxygen, nitrate, phosphate, non nitrogen-fixing phytoplankton, nitrogen-fixing phytoplankton (diazotrophs), zooplankton, and particulate phosphorus and nitrogen detritus. The experiments DOPU and COST (see below) additionally feature semilabile dissolved organic phosphorus and nitrogen. Water column denitrification is parameterized as a function of modeled oxygen concentrations. Benthic denitrification (BD) is not explicitly

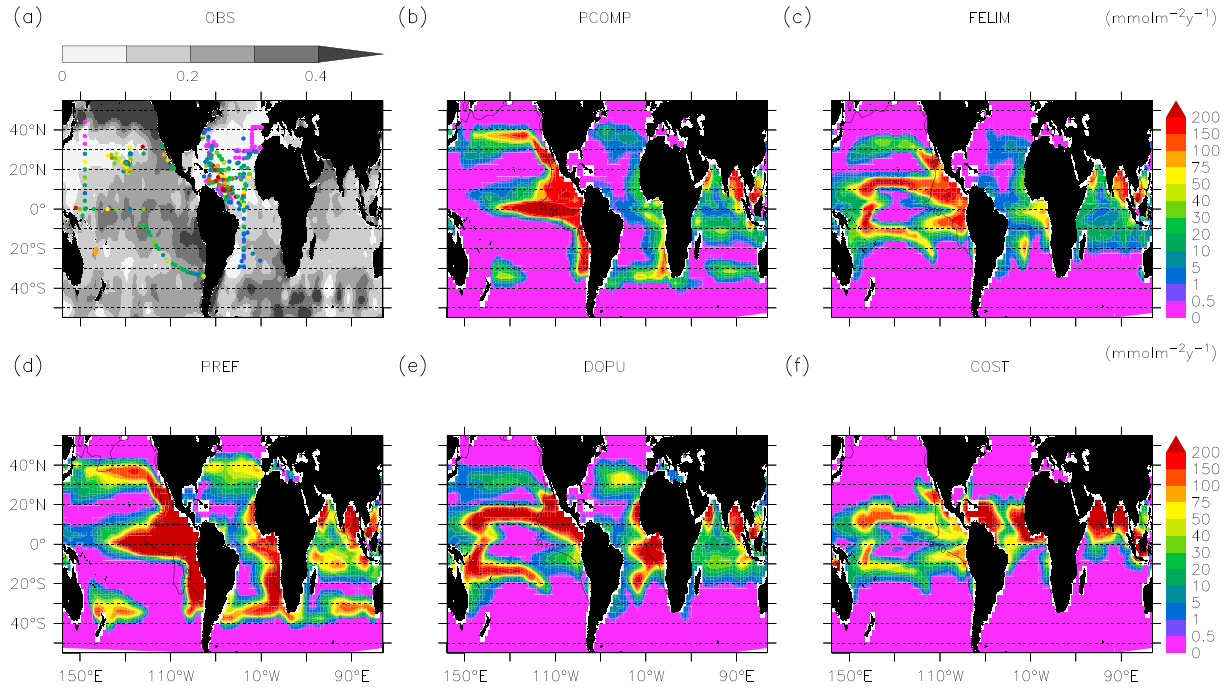

Figure 2. (a) Observed [*Luo et al.*, 2012] N_2 fixation (mmol N m^{-2} yr^{-1}; colored dots) and P* surface distribution (mmol P m^{-3}; grey shade) based on climatological data [*Conkright et al.*, 2002]. (b) N_2 fixation rates (mmol N m^{-2} yr^{-1}) from PCOMP, (c) FELIM, (d) PREF, (e) DOPU, and (f) COST simulations. Black contours represent the 0.1 mol N m^{-2} yr^{-1} denitrification isoline.

accounted for in our current model that does not resolve continental shelves. Fixing and nonfixing phytoplankton growth has a temperature dependence and is limited by light. Nonfixing phytoplankton is limited by PO_4^{3-} and NO_3^- using a Liebig-type limitation function. Diazotrophs are limited by PO_4^{3-} concentrations but can also take up NO_3^-. The maximum growth rate of diazotrophs is lower than that of nonfixing phytoplankton. To explicitly account for the additional energetic expenditure on Fe scavenging, the growth of both phytoplankton types can be further limited by an Fe limitation factor. Model simulations are restricted to

Table 1. Observed, Biogeochemical, and Modeled Global and Regional N_2 Fixation Estimates (Tg N yr^{-1})

Reference	Global (Tg N yr^{-1})	Pacific (Tg N yr^{-1})	Indian (Tg N yr^{-1})	Atlantic (Tg N yr^{-1})	NA (Tg N yr^{-1})	NA-Lat. °N
Luo et al. [2012][a]	137 ± 9	102 ± 20	-	34 ± 7	27[b]	0–30
Gruber and Sarmiento [1997][c]	110 ± 40	-	-	-	25[b]	0–30
Deutsch et al. [2007][d]	137	95	2 2	20	8[b]	0–30
Palter et al. [2011][e]	-	-	-	-	4.6–5.5	
This Study Model Experiment						
PCOMP	91	71	13	7	1.5	0–30
FELIM[f]	85(83 ± 7)	65(61 ± 8)	12(11 ± 0.6)	8(7.3 ± 0.2)	2.5(2.2 ± 0.5)	0–30
PREF	302	210	39	53	11	0–30
DOPU	170	110	25	35	12	0–30
COST[f]	134(198±106)	56(106 ± 68)	40(48 ± 24)	39(42 ± 22)	35(23 ± 12)	0–30

[a]Compilation of observational data.
[b]Areal rate extrapolated to the oligotrophic North Atlantic region (25 × 106 km^2).
[c]Geochemical estimate based on diazotrophic N:P of 125:1.
[d]Model-based geochemical estimate.
[e]Gyre-integrated rate estimated from excess phosphate supply.
[f]Numbers in brackets are the mean ± SD of sensitivity experiments described in supporting information.

150 years to limit model drift from observed nutrient and oxygen distributions. The results shown are from model year 150.

We conduct five model experiments:

1. PCOMP, where diazotrophs and nonfixing phytoplankton compete for PO_4^{3-}, is our simplest model configuration with no iron limitation and no dissolved organic matter dynamics.
2. In experiment FELIM diazotrophs and nonfixing phytoplankton growth rates are reduced by a moderate (MEDIUM, Figures S1c and S1d in the supporting information), spatially and seasonally varying, iron limitation factor. Sensitivities to different degrees of iron limitation (LOW and HIGH) have been carried out and are described in the supporting information.
3. In experiment PREF the particulate phosphorus remineralization rate is doubled in the top 143 m.
4. In experiment DOPU growth rates of both diazotrophs and nonfixing phytoplankton are reduced by a moderate iron limitation factor (Figures S1c and S1d) and diazotrophs can take up DOP as an alternative P source at no additional cost.
5. Experiment COST differs from experiment DOPU in that DOP uptake is associated with additional energy and N requirement, which apply to both nonfixing phytoplankton and diazotrophs. The extra energetic cost results in a 60% lower maximum growth rate relative to the DOPU run. The additional N requirement is such that for every P atom the N:P uptake ratio is 1.5 times the cellular N:P (16:1). The N taken up in excess of the cellular N requirement is released instantaneously as DON. The sensitivity of the results to different assumptions about costs in terms of N and energy is investigated and described in the supporting information.

3. Results and Discussions

When competing for PO_4^{3-} in our model experiment PCOMP, N_2 fixers are outcompeted by nonfixing phytoplankton in the North Atlantic (Figure 2b) where simulated N_2 fixation is low (1.5 Tg N yr^{-1}, Table 1) because of phosphate limitation (Figure S2a). The major share (78%) of the simulated global N_2 fixation (91 Tg N yr^{-1}) occurs in waters of elevated P* upwelling from oxygen minimum zones (OMZs) of the eastern equatorial Pacific. This is in line with the theoretical prediction [*Tilman*, 1980] and marine biogeochemical studies [*Redfield et al.*, 1963; *Tyrrell*, 1999; *Deutsch et al.*, 2007], which lead to suggest that marine N_2 fixation is spatially associated with sources of elevated P* caused by denitrification [*Deutsch et al.*, 2007]. However, the simulated low P* supply in the oligotrophic North Atlantic cannot support the N_2 fixation hot spot as observed in this region (Figures 2a and 3b). Additional surface P* may be provided by benthic denitrification (BD). However, models including this process suggest that BD does not contribute to fostering N_2 fixation in the oligotrophic North Atlantic [*Weber and Deutsch*, 2012]. This is consistent with observational estimates of relatively low rates of North Atlantic BD [*DeVries et al.*, 2013] and resulting P* supply [*Palter et al.*, 2011].

Taking the regional distribution of iron limitation into account in experiment FELIM, we find that iron limitation contributes to the accumulation (Figure S3a) and transport of P* (Figure 3c) from the OMZ-associated upwelling regions into noniron-limited waters, where it helps to reduce phosphate limitation of N_2 fixers (Figure S2b). When increasing the strength of iron limitation, global N_2 fixation is reduced, but regionally N_2 fixation increases in relatively iron-rich regions such as the North Atlantic (Figure 4a). The advective and vertical P* supply to the surface (Figures 3c and 3d) remains, however, insufficient to support observed levels of N_2 fixation in the tropical and subtropical North Atlantic (Figures 2a and 2c and Table 1).

Enhancing the availability of PO_4^{3-} by doubling the remineralization rate of organic phosphorus to PO_4^{3-} in experiment PREF augments surface P* (Figure S3b) and thereby global N_2 fixation rate (302 Tg N yr^{-1}, Table 1 and Figure 2d). However, as P* fluxes to the surface oligotrophic (0–30°N) North Atlantic remain low (Figure 3c and 3d), only 4% of the global N_2 fixation is simulated to occur in this region, still much less than observational estimates suggest (20%, Table 1). PO_4^{3-} availability may be enhanced also by stoichiometric diversity of nonfixing phytoplankton, which has been shown to expand the niche of N_2 fixers on a global scale [*Weber and Deutsch*, 2012]. A high cellular N requirement (large R) of nonfixing phytoplankton enlarges the region of $N:P_{supply} < R$ (high P* supply) (Figure 1a, larger α). We account for stoichiometric diversity in model experiment, nonRR, implementing two nonfixing phytoplankton types which differ in their maximum growth rates and in their N:P ratios, $R = 20$ and $R = 9$ respectively (Table S1), consistent with the stoichiometric plasticity of resource-limited and slow-growing and resource-replete and fast-growing phytoplankton, respectively [*Klausmeier et al.*, 2004; *Mills and Arrigo*, 2010; *Weber and Deutsch*, 2012]. In experiment nonRR we find that

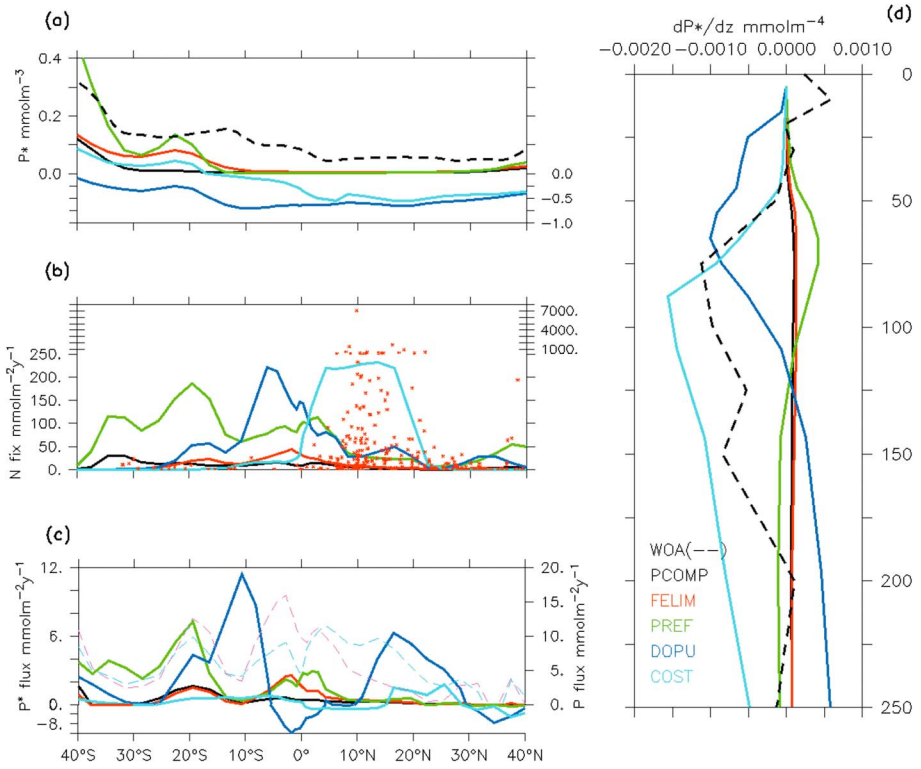

Figure 3. (a) Atlantic Ocean zonal average of climatological (dash) [*Conkright et al.*, 2002] and simulated surface P* (mmol P m^{-3}). (b) Observed (red star) [*Luo et al.*, 2012] and zonal average of simulated N_2 fixation (mmol N m^{-2} yr^{-1}). (c) Zonal average of simulated P* (solid lines, left *y* axis) and TP (PO_4^{3-} + DOP) (dashed lines, right *y* axis) advective flux (mmol P m^{-2} yr^{-1}). Pink line represents the COST simulation without the Fe limitation constrain. Please note broken *y* axes in Figures 2a–2c; labels are given in the left and right sides of the panels, respectively. (d) North Atlantic average (0–30°N) climatological and simulated vertical P* gradient.

the enhanced P* supply (Figure S4) is still insufficient to explain the observed patterns of Atlantic N_2 fixation (Figures 2a and 3b), in agreement with previous studies [*Weber and Deutsch*, 2012, supplementary Figures S2a and S2b].

Allowing for DOP uptake by N_2 fixers in experiment DOPU reduces their region of P limitation (Figure S2d) to the core of the subtropical gyres where modeled DOP concentrations are low (Figure S5b). The simulated global N_2 fixation (170 Tg N yr^{-1}, Figure 2e and Table 1) doubles compared to the simulation FELIM which does not include DOP dynamics. The largest increase occurs in the Pacific Ocean which contributes 65% to global N_2 fixation. Total P* fluxes to the surface oligotrophic North Atlantic (Figures 3c and 3d) support 12 Tg N yr^{-1}, 7% of the global N_2 fixation. However, the simulated distribution of N_2 fixation in the Atlantic Ocean does not match the observed latitudinal gradient (Figure 3b).

All mechanisms tested so far in our global model cannot maintain sufficient P* and DOP supply to support the elevated levels of N_2 fixation in the oligotrophic North Atlantic. To test a N-intensive DOP breakdown strategy [*Houlton et al.*, 2008], we account for the additional N and energy costs associated with exoenzymatic DOP breakdown by introducing an additional N demand and lower growth rates. We first apply resource competition theory (Figure 1). The extra N demand for the synthesis of extracellular enzymes requires N uptake in excess of the nonfixing phytoplankton's N:P ratio *R* (Figure 1b, black arrow, slope > *R*). We find that while N_2 fixers can easily satisfy the extra N demand, nonfixing phytoplankton become more N limited (Figure 1b, grey arrow). This expands the ecological niche of N_2 fixers into regions where $N{:}P_{supply} > R$ (Figure 1b, β; details in the supporting information, section 2). We now account for the costs for DOP breakdown in our three-dimensional global biogeochemical circulation model experiment COST. The additional N cost is simulated such that N demand exceeds the cellular N requirement by 50% resulting in N:P uptake ratio of 24:1. The associated energetic cost is simulated such that growth rate is reduced by 60% (see supporting information for details). Accounting for these trade-offs, N_2 fixation is stimulated in the tropical regions of the North Atlantic

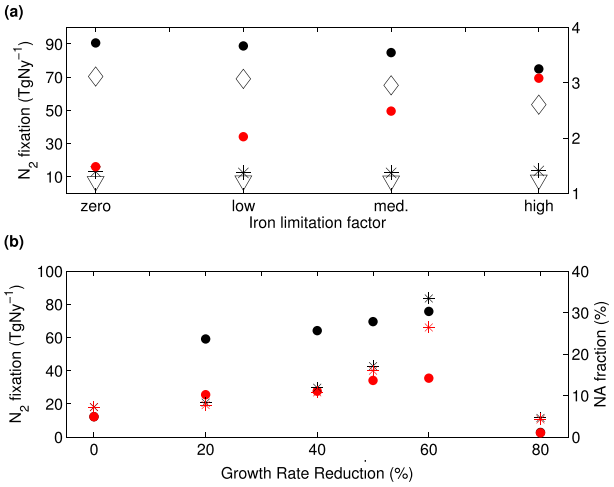

Figure 4. (a) Global and basin N_2 fixation rate (Tg N yr^{-1}) as a function of iron limitation factor in the FELIM experiment with the respective LOW, MEDIUM, and HIGH iron limitation factors. Zero corresponds to PCOMP experiment. Black dot = global, diamond = Pacific, star = Indian, inverted triangle = Atlantic, and red dot = North Atlantic (NA) (0–30° N). The second *y* axis is for North Atlantic data (and has the same units as the first *y* axis). (b) NA N_2 fixation rate (Tg N yr^{-1}) as a function of growth rate reduction for a 1.5 fold (red dot) and 2.5 fold (black dot) increase in the N cost in COST and its percent contribution (red asterisk), (black asterisk) to global N_2 fixation from the same experiments.

(Figure 2f) reaching 35 Tg N yr^{-1}, which is about 25% of the global N_2 fixation (134 Tg N yr^{-1}, Table 1). The additional energetic and N costs lead to a reduction of DOP-supported growth in waters above oxygen minimum zones reducing in turn particulate organic matter export, denitrification, and the associated P* resupply [*Landolfi et al.*, 2013]. We investigated the sensitivity of our results to variations of the N and energetic costs (details in the supporting information, section 1) and find that increasing these costs further enhances N_2 fixation in the North Atlantic and increases the contribution of the North Atlantic to global N_2 fixation (Figure 4b). Too high energetic costs (80% reduction of the growth rates), however, reduce the importance of DOP uptake as an alternative P source (Figure 4b). N_2 fixation simulated by our model is thus sensitive to the associated metabolic costs. Yet the inferred regional distribution of N_2 fixation appears robust in our model (Figure 4b and Table 1). The expansion of the niche of N_2 fixers into regions of low P* supply (Figure 3c) is possible as long as the N cost for DOP uptake is greater than the direct N supply by N_2 fixers (supporting information equation (25)), such that nonfixing phytoplankton growth remains limited by NO_3^-. In experiment COST the additional costs for DOP uptake relative to PO_4^{3-} uptake inhibit DOP uptake when PO_4^{3-} is available. The growth of both diazotrophs and nonfixing phytoplankton on DOP occurs in regions where DOP is a large fraction of the total dissolved phosphorus pool (>80%, Figures S5h and S6). This occurs in the oligotrophic, Fe-abundant, North Atlantic. In Fe-limited regions, the consumption of PO_4^{3-} and DOP is reduced because of Fe limitation. As a result, these nutrients can be transported from Fe-deplete into Fe-abundant regions (Figure 3c), where they can then fuel biological consumption by both diazotrophs and nonfixing phytoplankton. DOP is consumed, however, depending on phytoplankton's ability to cover the extra N costs associated with DOP uptake.

4. Conclusions

Our results offer a new perspective on the environmental controls of marine N_2 fixers. The competitive success of the slower-growing diazotrophs is generally associated with regions of N deficiency and of elevated P* supply, where the growth of their faster-growing competitors is suppressed. Here we show that diazotrophs can have a competitive advantage also in regions that are N rich relative to the cellular needs (*R*) of their faster-growing competitors. The additional energy and N costs associated with the enzyme-mediated hydrolysis of DOP favor N_2 fixers competitive success in PO_4^{3-}-starved regions. This strategy can explain the puzzling persistence of marine N_2 fixers in regions where estimated P* fluxes [*Palter et al.*, 2011] are insufficient to support observation-based N_2 fixation estimates. A N-intensive strategy for P acquisition in oligotrophic systems may also explain the widespread N limitation of phytoplankton [*Moore et al.*, 2013] as deduced from nutrient addition assays. Even in PO_4^{3-}-starved systems, experimental PO_4^{3-} addition fails to stimulate phytoplankton growth while N addition does [*Tanaka et al.*, 2011]. The addition of N is found to induce enzyme activity related to DOP hydrolysis [*Tanaka et al.*, 2011; *Mahaffey et al.*, 2014], suggesting a N-intensive strategy for P acquisition that ought to be explored. In our simulations Fe limitation prevents complete P consumption in Fe-limited regions and thereby allows a net transport of DOP and PO_4^{3-} into more Fe-replete regions where they may be consumed. Our findings suggest that global patterns of iron supply facilitate the potential for enhanced diazotrophy within the oligotrophic North Atlantic, while the additional nitrogen and energetic costs associated

with DOP hydrolysis provide diazotrophs with a competitive advantage for P in this relatively N-rich region. Understanding the factors regulating the distribution of marine N_2 fixation is essential if we are to predict changes in the oceanic N inventory.

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Erratum

In the originally published version of this article, some errors were identified in the text and in the Table 1 footnotes. The following have since been corrected, and this version may be considered the authoritative version of record.

In sections 1, 2 and 3, including the legends of Figures 2 and 3, all citations of *Conkright and Boyer* [2002] have been changed to *Conkright et al*. [2002], and this reference has been corrected in the reference list.

In section 2, "nonnitrogen-fixing" has been changed to "non nitrogen-fixing".

In Table 1, *Gruber and Sarmiento* [1997][b] has been changed to *Gruber and Sarmiento* [1997][c]; *Deutsch et al*. [2007][c] has been changed to *Deutsch et al*. [2007][d]; and *Palter et al*. [2011][d] has been changed to *Palter et al*. [2011][e]. Also, in the table footnotes, the former footnote [a] ("Areal rate") is now footnote [b], and the former footnote [b] ("Compilation of observational data") is now footnote [a].